OPEN ACCESS

University of BRISTOL

Miller, C. E., Pinkard, H., Johnson, L., & Schmitt, D. (2019). Pitch control and speed limitation during overground deceleration in lemurid primates. *Journal of Morphology*, *280*(2), 300-306. https://doi.org/10.1002/jmor.20944

Peer reviewed version

Link to published version (if available):
10.1002/jmor.20944

Link to publication record in Explore Bristol Research
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Wiley at https://onlinelibrary.wiley.com/doi/10.1002/jmor.20944 . Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research
General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/

Manuscript accepted for publication at the Journal of Morphology 18th December 2018

Formatted: Superscript

Pitch control and speed limitation during overground deceleration in lemurid primates.

Short title: Lemurid pitch control

Charlotte E. Miller[1]*, Henry Pinkard[2], Laura E. Johnson[3], Daniel Schmitt[4]

[1] Centre For Applied Anatomy, University of Bristol

[2] Center for Computational Biology, University of California, Berkeley

[3] Department of Pathology and Anatomical Sciences, University of Missouri

[4] Department of Evolutionary Anthropology, Duke University

***Corresponding author:** Charlotte E. Miller, Centre For Applied Anatomy, University of Bristol, 38 Southwell St, Bristol BS2 8EJ; charlotte.miller@bristol.ac.uk

Abstract

An animal's fitness is influenced by the ability to move safely through its environment. Recent models have shown that simple aspects of body geometry - limb length and center of mass (COM) position - appear to set limits for pitch control in cursorial quadrupeds. Models of pitch control predict that the body shape of these and certain other primates, with short forelimbs and posteriorly positioned COM, should allow them to decelerate rapidly while minimizing the risk of pitching forward. We chose to test these models in two non-cursorial lemurs: *Lemur catta*, the highly terrestrial ring-tailed lemur, and *Eulemur fulvus*, the highly arboreal brown lemur. We modeled the effects of changes in limb length and COM position on maximum decelerative potential for both species, as well as collecting data on maximal decelerations across whole strides. In both species, maximum measured decelerations fell below the range of pitch-limited deceleration values predicted by the geometric model, with the ring-tailed lemur approaching its pitch limit more closely. Both lemurs showed decelerative potential equivalent to or higher than horses, the only comparative model currently available. These data reinforce the hypothesis that a relatively simple model of body geometry can predict aspects of maximum performance in animals. In this case, it appears that the body geometry of primates is skewed towards avoiding forward pitch in maximal decelerations.

Key words: Lemur catta, Eulemur fulvus, Deceleration, Pitch, Arboreality

Graphical abstract text

Slowing down to a stop, possibly very quickly, is a vital part of primate behavior, but carries risks of tumbling forward 'over the handlebars'. The body shape of primates, particularly tree-dwelling species, may help to prevent these types of falls.

Introduction

The ability to accelerate and decelerate quickly to catch prey or avoid predation is critical to animal survival. Animals must be able not only to generate high speed through muscular effort, but also speed up or slow down without generating excessive pitching moments and causing the body to become unbalanced. The ability to control body pitch appears to be influenced by body proportions, at least in dogs and horses (Williams, Tan, Usherwood & Wilson, 2009). What remains an open question is whether other animals face such limitations, and whether the ability to control pitch is an important factor that constrains animal locomotor behavior, and exerts a selective pressure on limb anatomy.

In a defining paper on this topic Williams and colleagues (2009) demonstrated that at relatively slow speeds the need to control pitching moments is the primary limiting factor to maximum accelerations and decelerations in dogs and horses. In both these cursorial species the perils of 'popping a wheelie' while accelerating or 'diving over the handlebars' while decelerating appears to be a greater factor in limiting acceleration and deceleration at slower speeds than the limits potentially imposed by power production by limb extensor muscles (Williams et al., 2009). At higher speeds muscular power production becomes the primary limit to both acceleration and deceleration (Williams et al., 2009). Thus in their model, the key factor determining the theoretical limits of pitching moments is body shape,

specifically the ratios of limb lengths to their moment arm around the center of mass (COM), the latter defined as COM position as a proportion of back length (Williams et al., 2009, equation 1.1. Figure 1).

$$|\bar{a}_x| \leq \frac{gLcran}{Lfore} \qquad \textbf{equation 1.1}$$

Where $\bar{a}_x$ is the constraint placed on horizontal acceleration by forward pitch, g is the acceleration due to gravity, $Lcran$ the horizontal distance between the COM and the glenohumeral joint, $Lfore$ the length of the animal's forelimb. This equation explores in an elegant way the body geometry of animals and the effect of the ability to resist pitch by incorporating only aspects of limb length, body length, and COM position. When the value for $\bar{a}_x$ becomes greater than the ratio of gravity and COM position to limb length, forward pitching moments can no longer be countered, and the animal is in danger of going 'over the handlebars'. In this expression of the relationship mass would apply to both the $\bar{a}_x$ (forward acceleration) and g (vertical acceleration) terms, and would therefore cancel out. The data in Williams et al. (2009) show how effectively this equation predicts pitch limits for horses and dogs, including demonstration of high pitch in dogs such that they sometimes miss a forelimb footfall at the beginning of an acceleration event. Thus, under this model (Williams et al., 2009) the length of the limb and position of the COM have a profound influence over the range of decelerations an animal can achieve while avoiding uncontrolled pitch.

Although the role of center of mass placement in introducing pitching moments is easily understood and imagined (the further back the COM is on the body the more the body will resist being pitched over the forelimbs), the relationship between limb length and

COM position is less intuitive. Although it may seem sensible that long forelimbs would resist pitching, Williams et al. (2009) show that, all else being equal, longer limbs will increase pitching moments around the COM resulting in an animal vaulting over its forelimbs and pitching forward (nose-down) during deceleration. Therefore, the combination of short forelimbs and a posterior COM provides the greatest resistance to forward pitch during deceleration.

The model of Williams et al. (2009) appears to apply well to the cursorial mammals studied in acceleration (dogs and horses) and deceleration (horses) and provides important insight into selective pressures on body design. But it remains a question whether this model also applies to other, non-cursorial quadrupedal animals. Here we chose primates because of their adaptations to both terrestrial and arboreal movement. Primates are able to run effectively on the ground and some, including the ring-tailed lemur studied here, do so often. But primates also habitually walk and run on branches that are often small relative to their body size and present a complex and discontinuous substrate. Therefore, being able to avoid forward pitch is especially critical for their survival (even more so than avoiding the backward pitching risked with acceleration), and primates appear to have anatomical and behavioral adaptations for locomotion in an arboreal milieu (see Schmitt (2010) for a review). The ability to quickly stop without tumbling forward is a fundamental problem for all animals, but since it is especially critical for animals moving in trees, we propose to test the idea that primate locomotor behavior and limb proportions will reflect that priority, by avoiding issues of forward pitch during deceleration. Although great strides have been made in understanding how primates cope with challenges of steady state locomotion, decelerating remains a critical behavior which is not yet well studied, despite its

implications for a variety of behaviours that require decelerations for both stopping and turning maneuvers. This leaves a gap in our understanding of the selective pressures that influence primate body shape, as well as the factors which limit deceleration potential in primates.

Hence we predict that primates should show body proportions that allow them to decelerate over a wide speed range without excessive forward pitch. Primates are known to have anatomical features - including limb length and patterns of force distribution on the limbs - that distinguish them from most other quadrupedal mammals (see Schmitt (2010) for a review). Most non-primate mammals are described as having an anteriorly positioned COM, with greater vertical peak forces and vertical impulses on their forelimbs (See Lee, Bertram & Todhunter, 1999, Witte, Knill & Wilson, 2004, and Henderson, 2006 for examples in dogs, horses and, elephants), while most primates exhibit the opposite condition (Demes, Larson, Stern, Jungers, Biknevivius & Schmitt, 1994; Kimura, 1992; Kimura, Okada & Ishida, 1979; Vilensky & Larson, 1989; Reynolds, 1985), with a more posteriorly positioned COM, as evidenced by the higher weight support by the hindlimbs compared to their forelimbs. Expressed this way, in terms of force distribution, this difference can be seen as a dynamic, rather than strictly anatomical condition (for a discussion of the anatomical issues in primates see Vilensky and Larson 1989), which may be achieved by several possible mechanisms, including limb position, muscle activity, or relative limb compliance (Schmitt, 1999, Schmitt & Hanna, 2004; Larson & Stern, 2009, Raichlen, Pontzer, Shapiro & Sockol, 2009; Young, 2012).

These same variables may be critically important for pitch control since pitching moments are created by force application on the ground at some distance from the animal's

COM, the position of which is measured using the ratio of peak vertical forces between fore and hindlimbs. Furthermore, lemurid primates have relatively short forelimbs, both absolutely (Napier and Napier, 1967; Fleagle, 2013) and effectively (general observation from video and illustrations and confirmed by data within this paper): lemurid forelimbs, like many other primates, undergo high degrees of elbow flexion and yield during stance phase (Larney and Larson, 2004; Schmitt, 2010), shortening their effective limb length (Larney & Larson, 2004; Larson, Schmitt, Lemelin & Hamrick, 1999; Larson, Schmitt, Lemelin & Hamrick, 1999; Larson, Schmitt, Lemelin & Hamrick, 2001; Fleagle, 2013). There have been a variety of adaptive explanations for this combination of reduced peak loads and limb compliance, including the need to protect relatively gracile forelimbs and the requirements of locomotion and foraging on thin flexible branches (Schmitt & Hanna, 2004; Larney & Larson, 2004).

Here we suggest an additional adaptive phenomenon: that a more posterior COM and relatively short (absolutely and effectively) and compliant forelimbs compared to the hindlimbs provide lemurs and many other arboreal primates with particularly high pitch limits in deceleration, and therefore greater decelerative potential than other animals. This does not negate other ideas about primate limb form. Rather it suggests that primate limb behavior and anatomy may also be advantageous when decelerating. Although one must be cautious since lemurids do not represent all primates, understanding how their fundamental adaptations may also control pitch would lend additional information and hypotheses about the adaptive origin of primates in an arboreal environment.

To test these ideas, we chose two lemurid primate species to examine whether the ability to decelerate rapidly is influenced by body and limb design geometry in a non-

cursorial species in the way it appears to be in dogs and horses. This paper focuses on deceleration for both practical and theoretical reasons. First, we were able to collect a large sample of data on these primates slowing down from the maximum speed but considerably less data on acceleration to maximum speed. Secondly, following the models presently available (Williams et al., 2009), we hypothesize that relatively short (absolutely and effectively) forelimbs compared to hindlimbs of many primates and the relatively high peak hindlimb forces on those primates will enhance their ability to decelerate. These very factors may present an inherent tradeoff between deceleration potential and acceleration potential. As such, we see deceleration as a selective factor, particularly for those animals living in trees where changes in direction and discontinuities in substrate make being able to slow down rapidly without pitching over especially important. Therefore we focus on whether control of body pitch during deceleration appears to follow the same rules for these primates as it does for horses.

Materials and Methods

Animals: Our subjects were 3 individuals each from two species of strepsirrhine primates from the Duke Lemur Center (DLC) in Durham, NC: *Lemur catta* (Linnaeus, 1758) and *Eulemur fulvus collaris* (Geoffroy, 1796). All of the subjects were adult at the time of study, all three *Lemur catta* were male, two *Eulemur fulvus collaris* were male and one was female. The animals were maintained in accordance with United States Department of Agriculture regulations and with the National Institutes of Health Guide for the Care and Use of Laboratory Animals. Protocols were approved by the Institutional Animal Care and Use Committee of Duke University (#A319-10-12). Both species received

primarily fruit, vegetables, and monkey chow (Monkey Diet™, PMI Feeds, St. Louis, MO). Water was freely available, and animals were fed daily. The animals were housed socially in small groups of 2–6 animals, in large indoor enclosures (5–15 m^2 at the base, 5 m in height), which had suitable enrichment and natural light. There is an indoor portion of cinder block and chain link facing a hallway for husbandry staff and an outdoor portion enclosed by chain-link fencing that allowed exposure to the elements. The two portions are separated by a wall with small doors that are open during the day. Animals could enter and exit the indoor portion at will during the day. The enclosures include complex enrichment material. These include ropes, swings, suspended walkways, metal and plastic containers, durable rubber balls and other appropriate primate enrichment. The animals are attended to by DLC staff multiple times a day and thus have regular interactions both with their cage-mates and with humans. They are never handled aside from specific husbandry purposes. During warm months (April through October) animals often have access to large outdoor enclosures of multiple acres. Testing was carried out in a research room on an enclosed runway described below. Animals were captured by hand by DLC staff. Animals are trained for such captures and usually such events invoke minimal stress. They were carried in an appropriate animal carrier to the research room. Animals were never sedated or restrained in any way beyond the manipulation necessary to move them to the experimental area. No animals were sacrificed in this protocol. The experiment itself involved freely chosen movement speeds in a large enclosure and repeated food rewards. The food rewards are small pieces of fruit or nut meats matched appropriately to diet and limited so as not to affect appetite for normal feeding significantly.

196 Here we examine the effect of changes in effective limb length and COM cranio-
197 caudal position on pitch limits in two species of prosimian primate – the brown lemur,
198 *Eulemur fulvus*, and the ring-tailed lemur, *Lemur catta*. These two species are very similar
199 in size and morphology (see Fleagle, 2013 and Rowe, 1996 for a review). It is the case that
200 the grasping hands and feet of primates may allow them to counteract some of the pitching
201 moments associated with deceleration on arboreal supports (though see Schmitt & Lemelin,
202 2002 for some reason for caution with respect to hand postures and wrist flexion used by
203 arboreal animals), however, in order to directly compare maximal deceleration abilities of
204 prosimian primates against those calculated by Williams et al. (2009), we collected data
205 using a flat board rather than a raised pole. This model is designed to test the very simplest
206 case, absent other confounding factors, representing a first step towards understanding
207 primate deceleration. We recognize that behaviors on arboreal supports may vary from the
208 flat substrate and look forward in the future to examining those behaviors as well. At
209 present we are asking whether the model of Williams et al. (2009) applies to non-cursorial
210 animals running on the ground.
211 A total of 91 maximally decelerating strides were obtained from 3 adult *L. catta* (n
212 = 32) and 3 adult *E. fulvus* (n = 59). Animals moved freely along a 0.7 m wide x 2.1 m long
213 runway, and were video recorded at 60 Hz using a Sony Handycam (HDR-SR11, Sony,
214 Japan) placed at a distance of 2 meters perpendicular to their path of travel. Animals were
215 encouraged to move at a variety of speeds along a flat runway, and decelerated towards a
216 solid barrier which completely blocked their progress. Animals were allowed to walk and
217 run freely, and were encouraged to decelerate at their maximum comfortable rate from
218 whichever gait they chose. The animals were encouraged to move quickly away from one

end of the enclosure and travel toward the barrier. They often hurried away from the investigator when approached, and received food rewards after a complete traverse of the runway. The enclosure gave them room to reach comfortable speeds and take more than three full strides on the straight before encountering the barrier. However, the animals could begin their run at the back of the enclosure, following an elliptical race-track-like path before reaching the straight recording area. Animals were comfortable in the enclosure, having taken part in numerous studies in that environment over a period of several years. Observations of the same animals in this enclosure and in outdoor settings, along with comparison to previous studies on the same species (Franz, Demes & Carlson, 2005; O'Neill & Schmitt, 2012), gave us confidence that that animals were using fast walking and running speeds and decelerating near their maximum rate.

Initial velocity and deceleration across whole strides were obtained by digitization of the tip of the nose in DLT dataviewer (Hedrick, 2008) over two frames at limb touchdown (to obtain initial velocity) and the next touchdown of the same limb (to obtain final velocity). Total deceleration was obtained by subtracting final from initial velocity, divided by the time between these two events, and lead and trail limbs were assumed to be behaving symmetrically.

To examine the decelerative pitch limits for these species a range of limits were calculated using the methods of Williams et al. (Williams et al., 2009, equation 1, table 2). Forelimb and hip-glenohumeral joint length were measured in ImageJ (NIH, Bethesda, MD) from midstance values of both *L. catta* and *E. fulvus* during steady state walking as a conservative estimate of limb length. Two pitch limits were calculated for each species using mid-stance effective limb length values, and estimates of COM position (as a

proportion of back length) with either a non-primate-like COM position 'D_{COM}' (as used by Williams et al. (2009) using values from (Usherwood, Williams & Wilson, 2007), Figure 2, line D_{COM}, for sample curves see Figure 3), and an approximate primate-like COM position 'P_{COM}' (40% back length, based on dynamic COM values suggested by vertical force distribution in locomotion, Figure 2, line P_{COM}). Relative deceleration magnitudes were also calculated for each empirical data value as a proportion of the conservative dog-like pitch limits (D_{COM}) for each species.

To further explore the relationship between primate forelimb posture and COM location, the model was then varied for values of COM position between 30% and 80% of measured back length, and limb lengths between 80% and 120% of measured forelimb length values, forming a sensitivity analysis around estimates of potential posture changes (table 1, maximum estimated limit value Figure 2, line Max). Extreme pitch limit values were also calculated for values of COM position between 10% and 90% body length, and 50% and 150% limb length for comparison (table 1). This is a very conservative approach and produces a large range of possible values. As a result the pitch limits indicated in Figure 2 represent a broad spectrum of anatomical arrangements that might be considered to characterize the dynamic geometry of primates, with further extreme values available in table 1.

Linear regressions of deceleration versus initial velocity, Wilcoxon sum rank tests for differences between both relative and absolute deceleration magnitudes, and all model calculations were performed in MATLAB (R2012a, Mathworks, Natick, MA).

Results

Based on the geometric model used here (Williams et al., 2009), both lemur species have pitch limits that are relatively high (more negative) compared to previously published data for horses (Figure 2; Williams et al., 2009), which are the only data available for comparison. In such a direct comparison, without accounting for body size, it appears that lemurid species have the ability to achieve greater decelerations without inducing forward pitch compared to a cursor like the horse. A comparison across species of such significant body size differences should be viewed with caution, so we also compared within our sample; comparing the more cursorial and terrestrial species, the ring-tail lemur, with the more arboreal brown lemur. The calculated pitch limits are greater (more negative) for the more arboreal brown lemur than the ring-tailed lemur. Therefore, while a Wilcoxon sum rank test shows no significant difference in measured deceleration magnitudes between the brown and ring-tailed lemurs ($p = 0.34$), there is a significant difference between the two species in the measured deceleration values relative to the conservative pitch limit calculated from the geometric model ($p = 0.0054$; table 2). Neither species achieves decelerations which cross the conservative pitch limit (D_{COM}) predicted by our sensitivity analyses (Figure 2), though the ring-tailed lemur comes much closer to this limit than the brown lemur. In that context, the ring-tailed lemur exhibits a greater potential to pitch forward and fall than the brown lemur. Deceleration shows a significant increase with increasing speed in both species (table 3).

Discussion

The morphological and kinematic data recorded here for two primates, in conjunction with the pitch and muscle power limit model of Williams et al. (2009), suggest

that lemurid primates are especially well adapted to the challenges of managing pitching moments, and avoiding falling forward when decelerating. Lemurids share a bauplan with many other quadrupedal primates – relatively short (absolutely and effectively forelimbs compared to their hindlimbs, a relatively long back, and a more caudally positioned COM – that may be well suited to achieving rapid decelerations while avoiding forward pitch. Forward pitch associated with deceleration is inherently more hazardous than backward pitch associated with acceleration in terms of avoiding potentially fatal falls in a complex discontinuous environment. Indeed this body geometry may represent a significant tradeoff between deceleration potential and acceleration potential in arboreal animals, which warrants further study.

Conservative pitch limits on decelerative potential were calculated at -7.73 ms^{-2} and -5.74 ms^{-2} for the brown and ring-tailed lemurs respectively. These values are greater than those seen for the much larger horses studied by Williams et al. (2009, -3.89ms^{-2}). In decelerating horses a parabolic relationship was seen between deceleration and speed, with the inflection point at around 5.0 ms^{-1}, however at equivalent speeds (table 4) the decelerations of both lemur species continue to increase in magnitude (become more negative). Hence it may be the case that neither lemur is limited by the ability to produce the muscle power needed for successful deceleration within the range of speed values observed, as was seen in the horses. This is an area that deserves further study and a broader, size-matched comparative sample.

These results provide a new perspective on primate adaptations and open up areas for future investigation. Since the only available comparative model to date is the horse, a large, terrestrial animal likely operating at the opposite extreme to primates – prioritizing

acceleration abilities over deceleration since it habitually runs on flat ground – future work is needed to calculate values for intermediate species in both ecology and body size. It would also be remiss to ignore another primate feature - grasping hands and feet. The ability to use prehensile hands and feet to grip arboreal substrates may also play a large part in maintaining a primate's on-branch security, and may allow primates to counteract some of the pitching moments associated with deceleration. However, it is also possible that such a mechanism, relying on the coordination of incredibly fast reflexes and enough time for each footfall to transmit a sufficient quantity and direction of force, would be of limited effectiveness when coming to a sudden stop in such a precarious environment.

Finally, although not the main focus of this study, it is worth speculating on the effect of habitual substrate use in these two primates and the implications of these data for future studies. The brown lemur is almost exclusively arboreal, while the ringtail is the most terrestrial of all the prosimian primates, and exhibits gait mechanics that are more similar to those of a dog than those of the brown lemur (O'Neill & Schmitt, 2012). Though both lemurs exert higher peak forces on their hindlimbs compared to their forelimbs, the disparity is also more extreme in the brown lemur (Franz et al., 2005). The geometry of the brown lemurs, particularly their shorter forelimbs, gives them greater potential for deceleration without approaching the point where they are likely to fall forwards. Hence, while their absolute deceleration magnitudes are equal to those of the ring-tailed lemurs, their decelerations relative to their pitch limits are significantly smaller, potentially decreasing their chances of risking a fall. These data may hint at further evidence that arboreal animals may choose to 'play it safe' when it comes to locomotion, avoiding extreme behaviors which might cause perturbations on thin branches, destabilizing their

334 locomotor substrate and increasing their visibility to predators (Schmitt et al., 2006). We
335 propose here that this anatomical arrangement and mechanism of increasing safety while
336 decelerating may well be an important contribution to primates' success in arboreal
337 locomotion, and their adaptation to and radiation in an arboreal environment. This study
338 combined with that of Williams et al. (2009) suggest a productive area for further study in
339 other primates and cursorial and non-cursorial animals.
340

341 **Author Contributions and Acknowledgements**

342 Data are archived at Duke University on servers maintained by the Evolutionary
343 Anthropology Department and are available on request. We thank David Brewer and the
344 Duke Lemur Center for invaluable help with data collection, and Sarah Williams, Owen
345 Lovejoy, Ian Gilby, Roxy Larsen, Karyne Rabey and Angel Zeininger for helpful
346 comments on this manuscript. The authors declare no competing interests.
347

348 **References:**

349 Bishop, K.L., Pai, A.K. & Schmitt, D. (2008). Whole body mechanics of stealthy walking
350 in cats. *PLoS One 3*:e3808.

351 Demes, B., Larson, S.G., Stern, J.T., Jr, Jungers, W.L., Biknevicius, A.R. & Schmitt, D.
352 (1994). The kinetics of primate quadrupedalism: "hindlimb drive" reconsidered. *Journal of*
353 *Human Evolution*, *26*, 353-374.

354 Fleagle, J. (2013). *Primate Adapatation and Evolution* (3rd ed.). New York: Academic.
355 464p.

356 Franz, T.M., Demes, B. & Carlson, K.J. (2005). Gait mechanics of lemurid primates on
357 terrestrial and arboreal substrates. *Journal of Human Evolution, 48*, 199-217.

358 Hedrick, T.L. (2008). Software techniques for two- and three-dimensional kinematic
359 measurements of biological and biomimetic systems. *Bioinspiration and Biomimetics*
360 *3*:034001.

361 Henderson, D.M. (2006). Burly gaits: centers of mass, stability, and the trackways of
362 sauropod dinosaurs. *Journal of Vertebrate Palaeontology, 26*, 907-921.

363 Kimura, T. (1992). Hindlimb dominance during primates high-speed locomotion. *Primates*,
364 *33*, 465-476.

365 Kimura, T., Okada, M. & Ishida, H. (1979). Kinesiological characteristics of primate
366 walking: Its significance in human walking. In: Morbeck, M.E., Preuschoft, H., Gomberg,
367 N., (Eds.), *Environment, Behavior and Morphology: Dynamic interactions in Primates* (pp.
368 297-311). New York: G. Fischer.

369 Larney, E. & Larson, S.G. (2004). Compliant walking in primates: Elbow and knee yield in
370 primates compared to other mammals. *American Journal of Physical Anthropology, 125*,
371 42-50.

372 Larson, S.G., Schmitt, D., Lemelin, P. & Hamrick, M.W. (1999). The uniqueness of
373 primate forelimb posture during quadrupedal locomotion. *American Journal of Physical*
374 *Anthropology, 112*, 87-101.

Larson, S.G., Schmitt, D., Lemelin, P. & Hamrick, M.W. (2001). Limb excursion during quadrupedal walking: how do primates compare to other mammals? *Journal of Zoology, 255*, 353-365.

Larson, S.G. & Stern, J.T. (2009). Hip Extensor EMG and Forelimb/Hind Limb Weight Support Asymmetry in Primate Quadrupeds. *American Journal of Physical Anthropology, 138*, 343-355.

Lee, D.V., Bertram, J.E. & Todhunter, R.J. (1999). Acceleration and balance in trotting dogs. *Journal of Experimental Biology, 202*, 3565-3573.

Napier, J.R & Napier, P.H. (1967) A handbook of living primates. New York: Academic Press.

O'Neill, M.C. & Schmitt, D. (2012). The gaits of primates: center of mass mechanics in walking, cantering and galloping ring-tailed lemurs, *Lemur catta*. *Journal of Experimental Biology, 215*, 1728-1739.

Raichlen, D.A., Pontzer, H., Shapiro, L.J. & Sockol, M.D. (2009). Understanding hind limb weight support in chimpanzees with implications for the evolution of primate locomotion. *American Journal of Physical Anthropology, 138*, 395–402.

Reynolds, T.R. (1985). Mechanics of increased support of weight by the hindlimbs in primates. *American Journal of Physical Anthropology, 67*, 335-349.

Rowe, N. (1996). *The pictorial Guide to Living Primates*. New York: Pogonias.

Schmitt, D. (1999). Compliant walking in primates. *Journal of Zoology, 248*, 149-160.

Schmitt, D. (2010). Primate Locomotor Evolution: Biomechanical Studies of Primate Locomotion and Their Implications for Understanding Primate Neuroethology. In: Platt, M. & Ghazanfar, A. (Eds.), *Primate Neuroethology* (pp. 31- 61). London: Oxford.

Schmitt, D., Cartmill, M., Griffin, T.M., Hanna, J.B. & Lemelin, P. (2006). Adaptive value of ambling gaits in primates and other mammals. *Journal of Experimental Biology, 209*, 2042-9.

Schmitt, D. & Lemelin, P. (2002). Origins of primate locomotion: gait mechanics of the woolly opossum. *American Journal of Physical Anthropology, 118*, 231-8.

Schmitt, D. & Hanna, J.B. (2004). Substrate alters forelimb to hindlimb peak force ratios in primates. *Journal of Human Evolution, 46*, 237-252.

Usherwood, J.R., Williams, S.B. & Wilson, A.M. (2007). Mechanics of dog walking compared with a passive, stiff-limbed, 4-bar linkage model, and their collisional implications. *Journal of Experimental Biology, 210*, 533-540.

Vilensky, J.A. & Larson, S.G. (1989). Primate locomotion: Utilization and control of symmetrical gaits. *Annual Reviews of Anthropology, 18*, 17-35.

Williams, S.B., Tan, H., Usherwood, J.R. & Wilson, A.M. (2009). Pitch then power: limitations to acceleration in quadrupeds. *Biology Letters, 5*, 610-613.

Williams, S.B., Usherwood, J.R., Jespers, K., Channon, A.J. & Wilson, A.M. (2009). Exploring the mechanical basis for acceleration: pelvic limb locomotor function during accelerations in racing greyhounds (*Canis familiaris*). *Journal of Experimental Biology, 212*, 550-565.

Witte, T.H., Knill, K. & Wilson, A.M. (2004). Determination of peak vertical ground reaction force from duty factor in the horse (*Equus caballus*). *Journal of Experimental Biology*, *207*, 3639-3648.

Young, J.W. (2012). Ontogeny of limb force distribution in squirrel monkeys (*Saimiri boliviensis*): Insights into the mechanical bases of primate hind limb dominance. *Journal of Human Evolution*, *62*, 473–485.

Tables

Table 1. Pitch limits and pitch limit ranges. Calculated using equation 1.1, as derived from equation 1.1 of Williams et al. (2009). * denotes values displayed on Figure 2. D_{COM}, measured limb length and dog-like COM position (identical to the calculations of Williams et al., 2009), P_{COM}, measured limb length and primate-like COM position (based on, Max, maximum reasonable limit from COM position values between 30-80% back length, 80-120% limb length, with the minimum reasonable limit calculated from the same range of values. Maximum and minimum extreme limits as calculated from COM position values of 10-90% back length, 50-150% limb length.

	Brown lemur (ms^{-2})	**Ring-tailed lemur (ms^{-2})**
Dog limit (D_{COM}*)	-7.73	-5.74
Primate limit (P_{COM}*)	-10.54	-7.83
Minimum reasonable limit	-2.93	-2.17
Maximum reasonable limit (Max*)	-15.37	-11.41
Minimum extreme limit	-1.17	-0.87
Maximum extreme limit	-31.62	-23.48

436 **Table 2.** Means and standard deviations of decelerations. Deceleration means and standard
437 deviations, both absolute magnitudes and as proportions of the conservative pitch limits
438 calculated for each species. Sd, standard deviation, $n_{a\text{-}f}$, sample sizes from each individual.

		Mean	**Sd**
Absolute	*E. fulvus* (n = 59) (ms^{-2}) (n = 59; n_a = 16; n_b = 29; n_c = 14)	-2.07	1.20
	L. catta (n = 32) (ms^{-2}) (n = 32; n_d = 6; n_e = 10; n_f = 16)	-2.41	1.38
Relative	*E. fulvus*	0.27	0.15
	L. catta	0.42	0.24

439

440

Table 3. Linear regression equations, coefficients of determination (R^2) and sample sizes (n) for the two datasets of deceleration (negative acceleration) values with respect to velocity (V_0). In both species the slope of the regression line is significantly different from zero (t statistic) and the fit of the datapoints to the regression line is significant (f statistic).

	n	Linear regression equation	Coefficient of determination (R^2)	P-value (t statistic)	P-value (f statistic)
Brown lemur	59	y = -1.87x + 2.06	0.44	<0.01	<0.001
Ring-tailed lemur	32	y = -1.82x + 1.66	0.57	0.02	<0.001

449 **Table 4**. **Body parameters used in pitch limit modeling, and equivalent speeds for the**
450 **brown lemur, ring-tailed lemur and horse.** 3.0 ms^{-1}, the upper limit of speeds observed
451 in the slowest animal, a brown lemur, was used to calculate Froude numbers based on both
452 brown lemur hindlimb and forelimb length: a Fr of 2.1 for the hindlimb and 2.5 for the
453 forelimb. For comparison between brown and ring-tailed lemurs and the horse values
454 reported in Williams et al. (2009) equivalent speeds in ms^{-1} were back calculated from
455 these Fr values using limb lengths for the ring-tailed lemur and horse. Hence a brown lemur
456 travelling at 3.0 ms^{-1} is travelling at roughly the same relative speed as a ring-tailed lemur
457 moving at 3.7 ms^{-1}, and a horse moving at 7.6 ms^{-1}.

	Back length (m)	**HL length (m)**	**Speed (ms^{-1}) HL (Fr 2.1)**	**FL length (m)**	**Speed (ms^{-1}) FL (Fr2.5)**
Brown lemur (average)	0.26	0.20	3.0	0.14	3.0
Ring-tailed lemur (average)	0.32	0.32	3.7	0.24	3.8
Horse (Williams et al., 2009)	1.22	1.32	7.6	1.31	9.0

458

459
460

Figure Legends

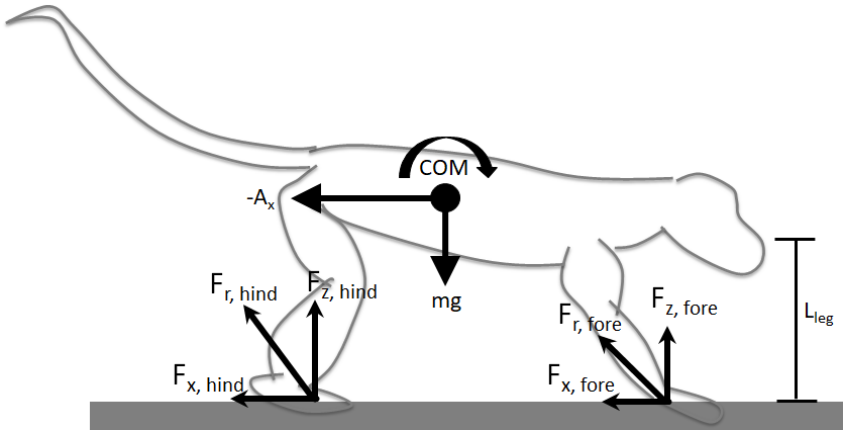


Figure 1. Modified from figures 1 and 2c of Williams et al. 2009 to show the effects of deceleration (rather than acceleration) on the COM (center of mass) of a generalized primate. More negative horizontal forces (F_x) will direct the GRF (ground reaction force) behind the COM and produce nose-down pitch. F_x, F_z and F_r represent horizontal, vertical and resultant ground reaction forces respectively, mg represents the vertical effect of gravity on the COM, $-A_x$ the negative acceleration of the resultant deceleration, and L_{leg}, the length of the forelimb.

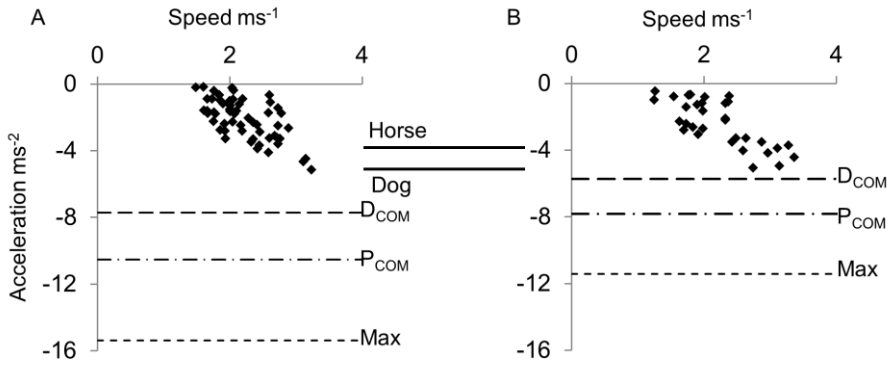


Figure 2. Deceleration versus velocity in brown and ring-tailed lemurs. A brown lemurs (N = 59) and B ring-tailed lemurs (N = 32). Pitch limits (D_{COM} and P_{COM}) are calculated using Williams et al. (2009, equation 1) using the measured forelimb length for each primate species (brown lemur in A, ring-tailed lemur in B, Table 4) and either a a dog-like center of mass (D_{COM}) or primate-like center of mass (P_{COM}).; Max, the maximum possible pitch limit defined by the conservative model; and for comparison: Horse, the pitch limit predicted for the horses used in Williams et al. (2009); Dog, the pitch limit predicted by the model of Williams et al. (2009) for a dog of average body geometry, calculated from published values (Usherwood et al., 2007).

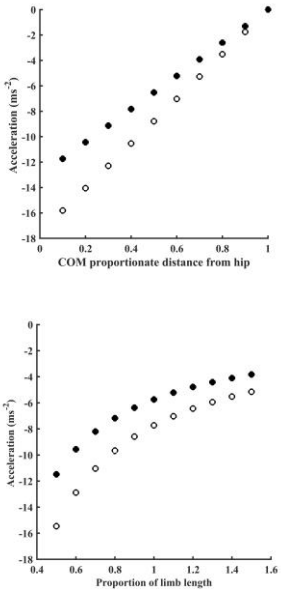
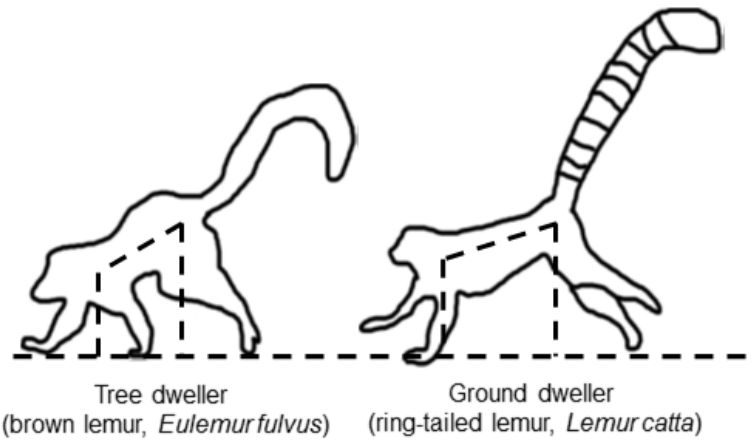


Figure 3. Sample sensitivity analyses. A. Sensitivity of deceleration limits calculated from equation 1.1 to changes in COM position for a measured limb length (Table 4). In the brown lemur (open circles), an animal with shorter forelimbs, there is a proportionately greater effect on pitch limits in deceleration when the COM is placed closer to the hip (where the left of the x-axis is closer to the hip, and right closer to the shoulder) as compared to the ring-tailed lemur (filled circles). B. Sensitivity analysis of deceleration limits calculated from equation 1.1 to changes in limb length for a given COM position (taken here as the 'non-primate-like position' of 56% Williams et al., 2009; Lee et al., 1999). Brown lemur values are seen in open circles, the ring-tailed lemur in filled circles. Shorter limbs have a proportionally greater effect on pitch limits (where the left of the x-axis shows shorter limbs, and the right longer limbs). Hence more crouched postures, those

seen often in quadrupedal primates (Schmitt, 1999) and stealthily walking cats (Bishop, Pai & Schmitt, 2008) increase pitch limits in deceleration. This effect is also seen in greyhounds during high accelerations (Williams, Usherwood, Jespers, Channon & Wilson, 2009).

Graphical abstract and graphical abstract text



Slowing down to a stop, possibly very quickly, is a vital part of primate behaviour, but carries risks of tumbling forward 'over the handlebars'. The body shape of primates, particularly tree-dwelling species, may help to prevent these types of falls.